

THE ORIGIN OF THE SILURIAN *CLARKEIA* SHELLY FAUNA OF SOUTH AMERICA, AND ITS EXTENSION TO WEST AFRICA

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ABSTRACT. The brachiopod *Aratanea monodi* Schmidt 1967 from Mauretania (West Africa) is put into the synonymy of *Clarkeia antisiensis*, chief constituent of the Malvinokaffric *Clarkeia* fauna of Central South America of Silurian age. The recently described fauna of latest Ordovician age from South Africa is considered to have been the ancestor of the *Clarkeia* fauna. In particular *Marklandella africana* is reassigned to *Heterorthisella*, and considered the ancestor of *Heterorthisella freitana*; *Plectothyrella haughtoni* is considered the ancestor of *Clarkeia* itself. *Eostropheodonta*, *Orbiculoidea* and homalonotid trilobites are common to both faunas. The ecology of both the South African and *Clarkeia* faunas is discussed. They are considered to represent the shallower end of the benthic depth spectrum, and may have been parallel communities to the contemporaneous *Hirnantia*, *Cryptothyrella* and *Eocoelia* Communities of Eurasia and North America. They may also have lived in colder water than the northern communities.

OVER the whole of the central part of South America there occurs commonly a fauna characterized by large numbers of a few genera of brachiopods, and dominated by the ribbed genus *Clarkeia* Kozłowski 1923. The age of this fauna has long been unsettled; it was originally thought of as Devonian, but now most workers agree that it is Silurian, and the age is discussed further below. This *Clarkeia* fauna has been described from Argentina (Kayser 1897, Thomas 1905, Castellaro 1959, 1967), Brazil (Clarke 1899, 1913) and Bolivia (d'Orbigny 1842, Kozłowski 1923). However, bearing in mind the exploratory state of geological knowledge in much of the South American hinterland, it may be expected also elsewhere in that general area. No other shelly Silurian faunas are known from this area.

The chief constituents of the fauna are brachiopods: *Clarkeia antisiensis* (d'Orbigny) in overwhelming numbers, together with scarcer *Heterorthisella freitana* (Clarke), *Eostropheodonta fascifer* (Kayser), *Australina jachalensis* Clarke, *Strophochonetes fuer-tensis* (Kayser), *Leptocoelia acutiplicata* Kayser, *Leptaena argentina* (Thomas) and various inarticulates, notably *Orbiculoidea* sp. Among other phyla *Tentaculites* sp., homalonotid trilobites, bivalves and gastropods have all been recorded sporadically. Material available in the British Museum (Natural History) includes a collection from Argentina made by the Shell Petroleum Company in 1961 and a collection from Bolivia recently presented by Professor Boucot. One of the problems in using some of the older literature cited above lies in disentangling the Silurian *Clarkeia* fauna from the genuine Devonian fauna which was in many cases simultaneously described from adjacent deposits.

All these brachiopod species, as well as the genera *Clarkeia* and *Australina*, are probably endemic to South America and West Africa, although more work is necessary on the *Leptaena*; and the fauna as a whole is noteworthy as being one of the few examples of possible provincialization in Silurian shelly faunas. As with the later Devonian province in the same general area, the term Malvinokaffric (Berry and Boucot 1972)

may be used. It is probable that the recently described *Ancillotoechia cooperensis* of Amos and Noirat (1971), from Jujuy Province, Argentina, is synonymous with *Clarkeia antisiensis*; their figured specimens appear identical to the Bolivian mould material figured in this paper.

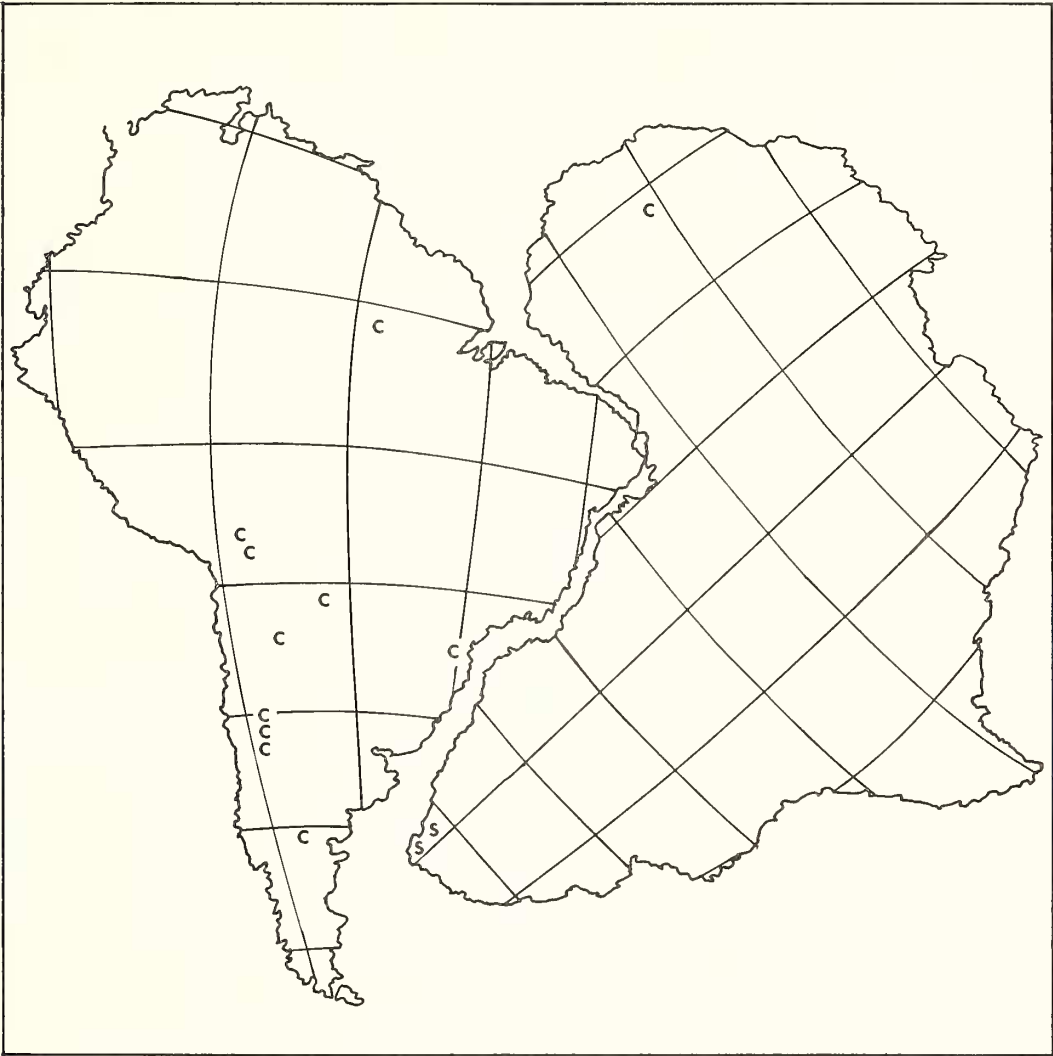
The *Clarkeia* fauna has not previously been reported from outside South America. However it can now be recorded from West Africa; in Mauretania in the western Sahara. These are the specimens described by Schmidt (1967) as *Aratanea monodi* gen. et sp. nov. A comparison of her excellent descriptions and figures leave no doubt that this form is identical with typical *Clarkeia antisiensis* (compare Schmidt 1967, pl. 1, figs. 1–6 with Plate 121, figs. 1–8 of the present paper). The stratigraphy of the Majâbat al-Koubrâ area was briefly described by Monod (1958) and consists of a sandstone containing large numbers of *Clarkeia* in an otherwise unfossiliferous sequence of clastic rocks. No other brachiopods are recorded. This form of occurrence is very similar to many in South America. The precise age of the fauna in Mauretania is not known; Monod (1958, p. 113) records the presence of graptolites further east, but these are not identified, and in any case their stratigraphical position relative to the 'Grès tendres à Brachiopodes' is not yet established.

The known occurrences of *Clarkeia* and its allies are plotted on a map (Fig. 1—redrafted after Bullard, Everett, and Smith) which shows South America and Africa in their relative positions before the Mesozoic to Recent continental drift occurred.

Also shown on the map is the position of the fauna described from South Africa by Cocks, Brunton, Rowell, and Rust (1970). These brachiopods, from the Cedarberg Formation of the Table Mountain Group, were described as *?Plectoglossa* sp., *Trematis taljaardi* Rowell, *Orbicnloidea* sp., *Marklandella africana* Cocks and Brunton, *Eostropheodonta discumbata* Cocks and Brunton and *Plectothyrella haughtoni* Cocks and Brunton. At the time that paper was written *Marklandella* Harper, Boucot, and Walmsley was an unpublished genus, but discussion with Dr. Walmsley and a brief look at their manuscript lead Dr. Brunton and myself to place the South African enteletacean within it. However, on fuller consideration of the published paper (Harper *et al.* 1969) and further discussion with Professor Boucot, I am now convinced that the Table Mountain Group species *africana* is better placed within another genus described in the same paper, *Heterorthella*. In particular *Heterorthella africana* (re-figured here, pl. 121, figs. 14–16) is considered to be a close relative of *H. freitana* (Clarke), one of the constituents of the *Clarkeia* fauna, particular emphasis being placed on the similarity of the shape of the muscle field in the pedicle valves, and the musculature and general valve form of the brachial valves. In the South African paper (Cocks *et al.* 1970, p. 594) we had remarked on the similarity of *africana* to '*Orthis*' *tacopayana* Kozłowski 1923; this latter species is now considered to be a junior synonym of *Heterorthella freitana* (Clarke 1899) (Harper *et al.* 1969, p. 80, pl. 16, figs. 1–6).

As further discussed in the systematic notes below, *Clarkeia* itself is very probably a close relative, and potential descendant, of *Plectothyrella* Temple 1965; in particular *C. antisiensis* is thought to be descended from *P. haughtoni* of the South African fauna (pl. 121, figs. 10–13). In addition *Eostropheodonta fascifer* of the *Clarkeia* fauna belongs to the same species group as *E. discumbata* from the Table Mountain Group, and the genus *Orbicnloidea* is common to both the *Clarkeia* and South African faunas. As to the other inarticulate brachiopods, it is possible that the form described as *Lingula* cf. *oblata* Hall by Clarke (1899, p. 8, pl. 1, fig. 3) may be comparable with the *?Plectoglossa* sp. of the South African fauna, but the inarticulates of the *Clarkeia* fauna are badly in need of expert taxonomic revision and redescription.

The age of the South African fauna is thought to be very close to the Ordovician–Silurian boundary, with the probability of an age just Ordovician, i.e. high Ashgill in European terms. The age of the *Clarkeia* fauna, discussed more fully below, is certainly Silurian. It is postulated here that the direct ancestor of this endemic *Clarkeia* fauna



TEXT-FIG. 1. Reconstruction of Africa and South America, prior to continental drift. Occurrences of *Clarkeia* (C) and South African (S) faunas are shown.

might very well have been the South African fauna from the Table Mountain Group, the latter being the starting point of the later, Silurian, minor provincialization.

AGE OF THE *CLARKEIA* FAUNA

The age of the *Clarkeia* fauna has given rise to much discussion. In the Los Espejos Formation of San Juan Province, Argentina, Cuerda (1965) has illustrated *Monograptus leintwardiunensis* var. *incipiens* Wood from beds with *Australina jachalensis*, and 600 metres above beds with *A. jachalensis*, *Clarkeia antisiensis*, and *Strophochonetes*

fuertensis. This graptolite, which seems correctly identified but should be termed *Saetograptus incipiens*, appears for the first time elsewhere in the basal Ludlow *nilssoniscanicus* Zone, and certainly suggests that the upper range of *A. jachalensis* extends to that age. However the fuller *Clarkeia* fauna 600 metres below is associated with what Cuerda identifies (but does not figure) as *Monograptus* aff. *vomerinus* (Nicholson). This suggests an age most probably in the lower half of the Wenlock for the *Clarkeia* fauna in that particular succession. This is the only reliable graptolite data associated with a *Clarkeia* fauna which have yet been published, although the presence of graptolites has been recorded elsewhere, some of which also suggest a Wenlock age. However, Helge L. Hansen has recently discovered graptolites in Paraguay of the *convolutus* or *sedgwickii* Zones of the Llandovery (*M. lobiferus* and *M.* aff. *sedgwickii*, identified by Dr. Rickards). These are associated with a shelly fauna, a very small sample of which includes poorly preserved ribbed atrypoids or rhynchonellides, *Lingula* and *Tentaculites*.

Internal age evidence is imprecise since all of the species, and the genera *Clarkeia* and *Australina* are endemic. *Clarkeia* is probably derived from the Ashgill and early Llandovery *Plectothyrella*; *Australina* is close to the Llandovery to Ludlow *Glassia*. As to the other genera, *Heterorthella* occurs only in the Ashgill of South Africa and the Wenlock of Canada, *Eostropheodonta* occurs from the Ashgill to the late Wenlock, although most commonly in the Ashgill; *Strophochonetes* occurs from the Ashgill to the Ludlow, although rare outside the Wenlock and Ludlow, and the remaining fauna suggest no more than a general Silurian age.

Perhaps the *Clarkeia* fauna may best be assessed as Llandovery to Wenlock in age, with a few elements such as *Australina* persisting into the Ludlow. The age span of the fauna is not clear; whether it persisted in different areas through the Llandovery and

EXPLANATION OF PLATE 121

- Figs. 1–8. *Clarkeia antisensis* (d'Orbigny). Figs. 1, 4 from San Juan Province, Argentina, collected Shell Petroleum Company 1961, Figs. 2, 3, 5–8 from Arquillos, near Tomina, Chuquisaca Department, Bolivia. Figs. 1, 4, BB 51599, external views showing ribbing, high shoulders and fold and sulcus, $\times 2.0$. Figs. 2, 7, BB 34263, oblique view of internal mould of both valves, and latex cast of the umbonal area showing erect crural lobes, $\times 3.0$. Fig. 3, BB 34264, internal moulds of several valves illustrating rock-forming abundance, $\times 2.0$. Fig. 5, BB 34265, latex cast from internal mould of conjoined valves, showing cruralia; the shadow reveals their form, $\times 3.0$. Fig. 6, BB 34266, latex cast from internal valve of conjoined valves, oblique view showing massive cardinal process projecting posteriorly, $\times 3.0$. Fig. 8, BB 34268, latex cast of pedicle valve interior, showing muscle field and laterally flaring rims from the teeth, $\times 3.0$.
- Fig. 9. *Plectothyrella crassicosta* (Dalman), BB 31867, the conjoined valves figured by Wright (1968, fig. 4) from Ashgill mudstones within Kildare Limestone, knoll west of Chair Farm, County Kildare, Ireland, $\times 1.5$.
- Figs. 10–13. *Plectothyrella haughtoni* Cocks and Brunton, from Cedarberg Formation, Wellington Sneekop, Cape Province, South Africa, collected by I. C. Rust. Fig. 10, BB 31528, posterior view of brachial valve internal mould, $\times 1.5$. Fig. 11, BB 31566, holotype, latex cast of a brachial valve internal mould, showing anteriorly directed crural lobes, $\times 2.0$. Fig. 12, BB 31527, posterior view of brachial valve internal mould, $\times 2.0$. Fig. 13, BB 31529, latex cast of brachial valve internal mould, showing vertical and stubby crural lobes, $\times 2.0$.
- Figs. 14–16. *Heterorthella africana* (Cocks and Brunton), from Cedarberg Formation, Langvlei, near Porterville, Cape Province, South Africa, collected by I. C. Rust. Figs. 14, 15, BB 31601, internal mould of brachial valve and latex cast of it, $\times 2.0$. Fig. 16, BB 31582, internal mould of pedicle valve, showing shape of muscle field, $\times 2.0$.



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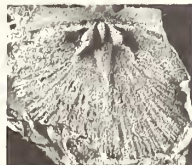
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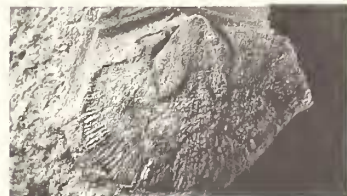
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Wenlock or whether all the fauna occurred at a similar time is unknown. As can be seen from the lists of Castellaro (1967, pp. 13–20), not all the elements of the *Clarkeia* fauna occur at all the localities; perhaps future work may enable further separation to be made. Berry and Boucot (1972) also discuss the age problem.

ECOLOGY

In the European Upper Llandovery five shelly assemblages have been defined, which are considered to reflect the marine benthic communities of that time (Ziegler, Cocks, and Bambach 1968). They were distributed according to some direct function of depth, chiefly because they map out as bands subparallel to palaeo-shorelines. As with their modern marine level-bottom counterparts, the diversity of animals within the communities increases from the shallow to the deeper part of the bathymetric range. Thus the fairly shallow-water *Eocoelia* Community usually has no more than six or seven species of brachiopod, in addition to some molluscs, a few bryozoa, *Tentaculites* and rather rare trilobites (usually either *Dalmanites* or *Encrinurus*). In contrast the *Clorinda* Community, at the other end of the depth spectrum, may have as many as thirty brachiopod species represented, as well as many other animals. In the lower part of the Llandovery *Eocoelia* itself does not occur, and the place of the *Eocoelia* Community is taken by the *Cryptothyrella* Community, such as occurs in abundance in the Mulloch Hill Formation of Girvan, Scotland.

In the late Ashgill there occurs another most distinctive fauna, once again dominated by brachiopods, called the *Hirnantia* fauna, after a common enteletacean. This occurs in Poland (Temple 1965), Bohemia (Marek and Havlíček 1967), Sweden (Bergström 1968), Great Britain and Ireland (Wright 1968) and in North America (Boucot and Johnson 1970). The *Hirnantia* fauna has several elements in common with the South African fauna, in particular *Plectothyrella haughtoni* from the Table Mountain Group is related to *P. crassicosta* (Dalman) (pl. 121, fig. 9), and *Eostropheodonta discumbata* from Africa is close to *E. hirnantensis* of the *Hirnantia* fauna. *Orbiculoidea* and homalonatid trilobites occur in both faunas. Although the composition and structure of late Ashgill shelly communities has not yet been fully evaluated, it is reasonable to postulate that the low-diversity *Hirnantia* fauna represents a community filling a comparable ecological niche to the *Eocoelia* and *Cryptothyrella* Communities of the lower Silurian.

Another relevant assemblage, just described from the upper Ashgill 'Grès du deuxième Bani' of Morocco (Havlíček 1971), consists of *Hirnantia sagittifera*, *Eostropheodonta squamosa* (very close to, if not conspecific with *E. discumbata*), *Destombesium zagoraensis* and *D. ellipsoides* (new enteletacean taxa), and a new species of *Plectothyrella* named *P. chauveli*. Unfortunately the material is scarce and rather poor, but this last species appears to be morphologically intermediate between *P. crassicosta* and *P. haughtoni*. This assemblage is of interest as being the first *Hirnantia* fauna described from Africa, and one providing suggestive links between the typical *Hirnantia* fauna and the fauna from South Africa.

The South African and *Clarkeia* faunas also have low diversity indices. Two explanations are possible; firstly, that the two southern hemisphere faunas lived in shallow water, in a similar way to the European and North American communities, and can therefore be considered as parallel communities to the northern ones; and secondly, that the low

diversity of the southern faunas was due to cold-water conditions, perhaps corresponding to some Arctic faunas today. There is certainly good evidence of a late Ordovician–early Silurian glacial period in both north and south Africa (Destombes 1968, Cocks *et al.* 1970). However, no elements of the South African fauna are more than specifically distinct from European faunas, and it seems most likely that that fauna at least was a relatively shallow-water one, parallel to the *Eocoelia* and *Hirnantia* Communities. Whether the same is true of the *Clarkeia* fauna remains at the moment equivocal: there is evidence of a glacial period in Argentina and Bolivia, but not from Brazil or the Sierra de la Ventana of Argentina (Berry and Boucot 1972); but a shallow-water sea over the area populated by the *Clarkeia* fauna seems a fair hypothesis in our present state of knowledge.

SYSTEMATIC NOTES

Several authors have discussed the problems in distinguishing ribbed atrypidines and rhynchonellides during the Ordovician and Silurian. The only objective difference between the two groups is the presence of calcareous spiralia supported by a jugum in the atrypidines and their absence in the rhynchonellides. The situation is further complicated by the rhynchonellides' probable position as the parent stock of the atrypidines. The practical difficulty lies in ascertaining whether a particular brachiopod genus had spiralia; their absence in any given specimen being so often due to the vagaries of preservation.

Fortunately perfect *Clarkeia* material was available from San Juan province, Argentina (pl. 121, figs. 1, 4), some specimens of which were serially sectioned after calcining. Long rhynchonellide crura, which ended in very fine subparallel blades, were completely preserved. There was no trace of spiralia or any jugal apparatus, which would certainly have been seen in this fine preservation. This confirms the conclusion suggested by the Bolivian mould material (pl. 121, figs. 2, 3, 5–8), and by Schmidt's work (1967), that *Clarkeia* is a rhynchonellide. *Plectothyrella* material completely preserved in calcite and suitable for sectioning has not been available, and so the presence of spiralia in that genus is still in doubt. Bergström (1968) and Boucot and Johnson (1970) both suggest that it is a rhynchonellide, as opposed to Temple (1965), Boucot and Johnson earlier (see 1970, p. 894) and Cocks *et al.* (1970) who believed it to be an atrypidine, perhaps related to the morphologically similar genus *Clintonella* Hall, from the Lower Silurian of North America, which has spiralia. However, it is here proposed that *Plectothyrella* is more closely related to *Clarkeia* than to any other genus; they seem best united in the subfamily Plectothyrellinae which was erected by Bergström (1968), and included in the rhynchonellides. Schmidt (in Williams *et al.* 1956, p. H570) includes *Clarkeia* in the Eatonidae. Dr. G. A. Cooper has very kindly sent on exchange some specimens of *Eatonia medialis* (Vanuxem), the type species of the family, as well as some *Costelloirostra peculiaris* (Conrad) for comparison. It seems reasonable to include the Plectothyrellinae as a subfamily within the Eatonidae, rather than in the Ancistorhynchidae as suggested by Bergström (1968), although Silurian rhynchonellides as a whole need systematic reappraisal.

Clarkeia antisiensis and *Plectothyrella haughtoni* are closely related and probably descended from one another. The differences between them are as follows. *Clarkeia* has a massive cardinal process, usually projecting posteriorly and sometimes bifurcating at the end; *P. haughtoni* has almost no cardinal process, and the diductor muscles must